TRAVAUX DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE «GRIGORE ANTIPA»
THE JOURNAL OF "GRIGORE ANTIPA" NATIONAL MUSEUM OF NATURAL HISTORY

Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 67 (2): 463–472 (2024)
doi: 10.3897/travaux.67.e120117

RESEARCH ARTICLE

Orbital asymmetries in tamarins of the genus *Saguinus* (Primates, Callitrichidae)

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Received 2 February 2024 | Accepted 11 June 2024 | Published 31 December 2024

Citation: Parés-Casanova PM, Vélez-García JF (2024) Orbital asymmetries in tamarins of the genus *Saguinus* (Primates, Callitrichidae). Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 67(2): 463–472. https://doi.org/10.3897/travaux.67.e120117

Abstract

The aim of this study was to analyse the orbital asymmetry in *Saguinus* skulls. The examination was conducted on 13 dry well-preserved skulls, belonging to different species of the genus *Saguinus*. The sample was studied by means of geometric morphological methods. The photos were taken by a digital camera with high definition. Digital pictures were obtained on the facial plane of each skull, and subsequently 15 semi-landmarks were placed along each orbital ridge. Contralateral orbital asymmetries were compared individually for both size and shape. Interestingly, we discovered statistically significant differences in size, which can be interpreted as orbital area, with the right orbit being larger, as well a significant shape directional asymmetry, which changes affected mostly the lacrimal and temporal edges. Detected orbital asymmetry can be assumed as a normal although unconspicous anatomic adaptative pattern in *Saguinus*, as it has been described in other primates. The underlying causes remain unknown, although this directional bias may indicate a possible visual lateralization. This is the first demonstration of orbital form asymmetry in this genus.

Keywords
directional asymmetry; eye dominance; fluctuating asymmetry; Neotropical primates.

Introduction

During many years, it has been believed that lateralization was an unique characteristic of humans (Warren 1980) but recently, many studies have shown that side preferences

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extends to many vertebrates, including amphibians and reptiles (Butcher and Blob 2008) (Malashichev 2016), tetrapod mammals (Austin & Rogers, 2012) (Siniscalchi et al. 2014) (Phillips et al. 2015) (Svoke 2017) (Camerlink et al. 2018) (Giljov et al. 2019) and primates other than humans (Fagot and Vauclair 1991) (Braccini et al. 2012), all exhibiting different levels of laterality. There have been described two main expressions of laterality: motor laterality and perceptual laterality (Braccini et al. 2012). Motor laterality is related to movement and physical tasks, while perceptual laterality is related to ear and eye functions (Braccini et al. 2012). The latter is related to the reception and transmission of sensory information to the central nervous system (Farmer et al. 2010). A lateralized visual domain may indicate lateralization in the processing of this information (Giljov et al. 2019).

Morphometry has been an instrument for the study of the shape of biological structures (Adams et al. 2013). Historically, morphometry has used the collection and analysis of distances or angles through basic instruments such as the calliper and the goniometer (Richtsmeier et al. 2002). Geometric Morphometrics (GM) describes shape using sets of coordinates of anatomical points (landmarks and semi-landmarks) (Zelditch et al. 2004). GM also allows to generate drawings as a support in the interpretation of the results. Asymmetry over time has been estimated using different indices with varying degrees of reliability (Bartosiewicz et al. 1993). In relatively recent times, asymmetry analysis has begun to be focused through GM (Rohlf and Bookstein, 1990). Fluctuating asymmetry (FA) is a type of bilateral asymmetry (Klingenberg 2015) characterized by minor non-directional (i.e., random) deviation from zero of the differences between the values of the corresponding right and left parts (Graham et al. 2010). Directional asymmetry (DA) is another type of asymmetry characterized by a statistical predominance of either right or left part (Kubicka et al. 2016).

Tamarins or long-tusked marmosets are platyrrhine primates of the family Callitrichidae belonging to genus *Saguinus and* closely related to the Lyon tamarins of the genus *Leontopithecus* (Ankel-Simons 2007) (Rylands et al. 2016). They are found in the forests of South and Central America, from the Amazon basin, Guianas to northern Colombia and Panama (Hearn 1983) (Defler 2010) (Rylands et al. 2016). These primates are diurnal and arboreal with frugivorous-insectivorous feeding habits (Hearn 1983; Rylands et al. 2016). Similar to other primates, they have also colour vision, since different cone pigments have been detected (Jacobs, 2008). Having eyes located on the front of the head (Ankel-Simons 2007), *Saguinus* have a wide binocular camp (Dyce et al. 1999), which provides them with a good visual accuracy. Their orbits are located medially and their margins are formed by the frontal, zygomatic, lacrimal and maxillary bones (Ankel-Simons 2007).

The skull of this genus has been studied to discern evolutionary processes from craniofacial variation, stating that the tamarin dispersal come mainly from south to north (Ackermann and Cheverud 2002). The purpose of this research was to assess the asymmetry of the orbit in the genus *Saguinus* with the application of GM techniques. Any kind of research on the genus *Saguinus* is important, since some

species are included on the list of endangered species by the IUCN (International Union for Conservation of Nature and Natural Resources) (Defler 2010).

Material and methods

A total of 13 adult dry skulls of various species of the genus *Saguinus*, in good preservation state, were studied:

Saguinus lagonotus	1
Saguinus fuscifollis	2
Saguinus nigricollis	1
Saguinus imperator	1
Saguinus leucopus	1
Saguinus midas	2
Saguinus nigeur	1
Saguinus oedipus	1
Saguinus sp.	3

Skulls with evidence of trauma, malformations or other pathologies had been previously excluded. Specimens are currently deposited in the collection of the *Museu de Zoologia* de Barcelona (Catalonia, Spain), and the Veterinary Anatomy Laboratory of the Faculty of Veterinary Medicine and Zootechnics of the *Universidad del Tolima* (Ibagué, Colombia).

A facial photograph of each skull was obtained with a Nikon digital camera (D5100) equipped with an objective AF-S DX Micro Nikkor 40mm f/1·2.8G. The skulls were fixed and levelled with clay to make it easier for the facial plane to be parallel to the camera's focal plane. A millimetre pattern was included in each image. Distances to the skull could vary between specimens but they were always below 30 cm.

Representing the shape of a structure by setting landmarks (anatomical points) can leave out important aspects such as curvature. Curvature is an inherent feature of the shape and is maintained after filtering the effects of localization, scale, and translation (Gunz and Mitteroecker, 2013). The orbit is a complex curve structure with no clear points for anatomical landmarks, so no reliable method exists to measure orbital ridge. Thus, 15 semi-landmarks along the orbital edge of each side were considered (Figure 1). Unlike landmarks, semi-landmarks are discrete points that are initially obtained as coordinates on an initial curve, and then transformed into equidistant discrete points (Gunz and Mitteroecker 2013). The set of semi-landmarks was obtained in each orbit with the application of the software tpsDig2 v. 2.16 (Rohlf 2015a) and posteriorly, with the program tpsUtility v. 1.70 (Rohlf 2015a), they were transformed to landmarks. Two replicas were obtained for each individual, as always suggested for the study of asymmetries (Klingenberg 2015). These two sets were carried out by the first author (PMPC).

Shape and size analyses were performed using GM techniques. To assess whether the variation between the two spaces (Euclidean and tangent) was minimal, correlations between the tangent distances and the Procrustes distances were also computed using the tpsSmall v. 1.33 application (Rohlf 2015b). The result of this correlation (0.99999) confirmed that both spaces were almost identical. A generalized full Procrustes fit was performed on two-dimensional landmark coordinates to extract shape information. The Procrustes fit with reflection of shape mapped the right and left shape orbital configurations together and Procrustes distance was used as a measure of shape asymmetry between the right and left side (Klingenberg et al. 1998). After configurations were scaled to unit centroid size (CS computed as the square root of the sum of squared distances of all landmarks from the centroid (Bookstein 1991)), configurations were rotated around their centroid (the point with average coordinates). The shape in this context is defined as the information that remains after the set of coordinates have been removed (Zelditch et al. 2004). Centroid size in this research it can be interpreted as orbital area.

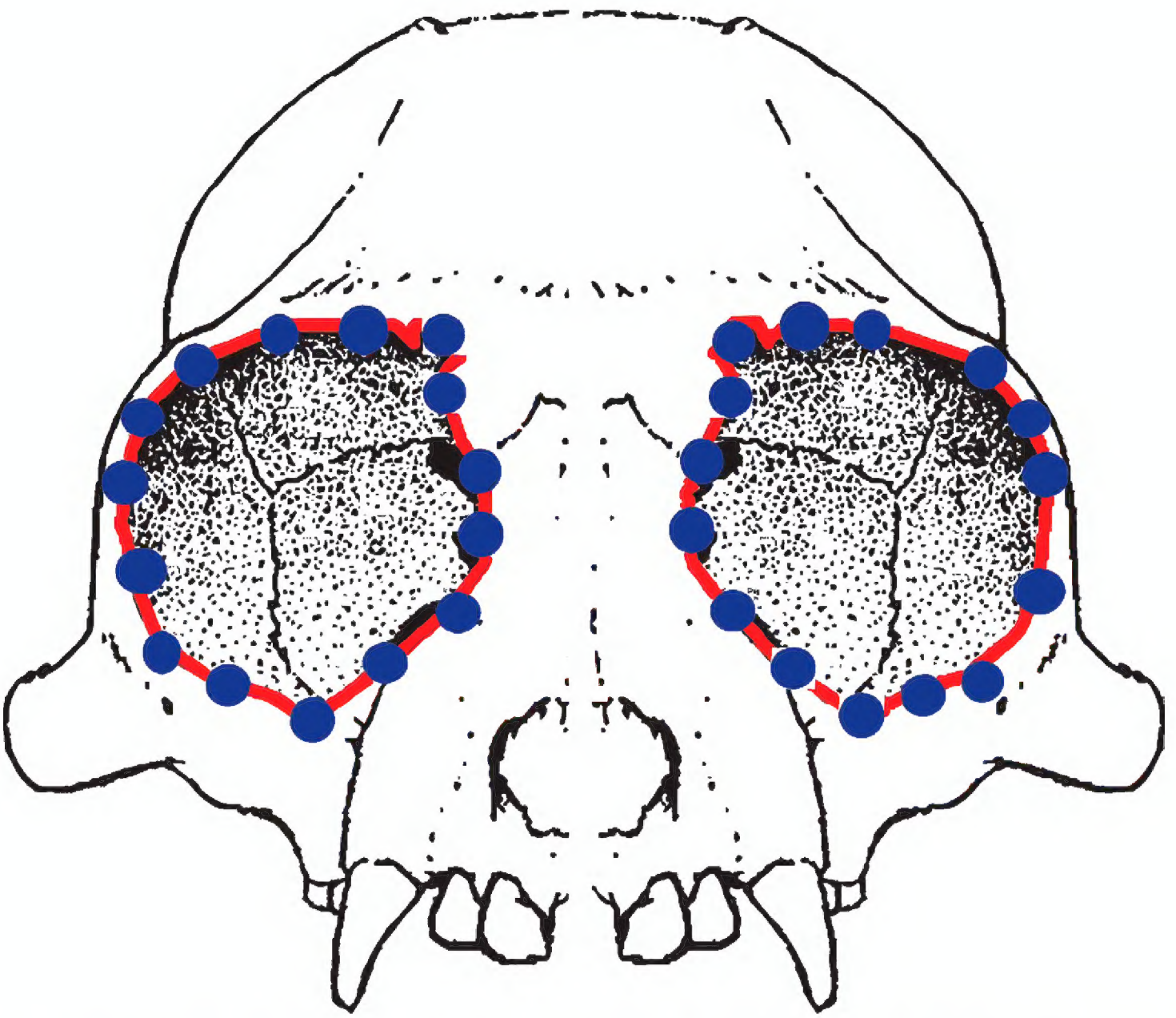

Figure 1. Used 15 semi-landmarks along the orbital edge of both sides in the skull of *Saguinus*. Semi-landmarks were ulteriorly transformed into equidistant discrete points.

To determine size and shape asymmetries, a multivariate analysis of the variance was performed on the contralateral coordinates of the orbits. The model allowed simultaneous to evaluate the effect of laterality (DA) and the individual*laterality interaction (FA). The direction of size asymmetry was obtained by a comparison of centroid sizes between pairs of orbits using a Wilcoxon *W* paired test, as data were not normally distributed. Since a significant regression was reflected between the size (centroid size, logarithmically transformed) and shape (Procrustes coordinates) (p=0.0120; 10,000 iterations), the last test, a Principal Component Analysis was performed with the residuals of regression. A representation of bending energy (thin plate spline) allowed finally to appreciate shape changes as forces acting on a mesh that deforms according to the sense (positive or negative).

Data was analysed in MorphoJ software v. 1.6.0c (Klingenberg 2011) and PAST v. 2.17c (Hammer et al. 2001). The statistical significance level was set at 95%.

Results

Size asymmetries

The Wilcoxon paired test reflected statistically significant differences in the size of the orbits (W=287, p=0.0036), as well as the results of ANOVA (Table 1), with the right size orbit being about a 1.2% larger (Figure 2).

Table 1. ANOVA results for pure size and shape. The model allows simultaneous evaluation of the effect of laterality (directional asymmetry) and the individual*laterality interaction (fluctuating asymmetry). SS: sum of squares; MS: mean squares; d.f.: degrees of freedom; F: value of the statistics F; SS and MS are expressed in units of distances Procrustes (i.e. dimensionless).

A/ Size Effect	**SS**	**MS**	**d.f.**	**F**	**P**
Individual	106.2879	8.857324	12	17.36	<0.0001
Laterality	4.778304	4.778304	1	9.36	0.0099
Individual*laterality	6.123086	0.510257	12	84.47	<0.0001
Error	0.157055	0.006041	26		

B/ Shape Effect	**SS**	**MS**	**d.f.**	**F**	**P**	**Pillai**	**P**
Individual	0.470697	0.001509	312	1.45	0.0005		
Laterality	0.236671	0.009103	26	8.75	<0.0001		
Individual*laterality	0.324568	0.001040	312	47.09	<0.0001	11.69	<0.0001
Error	0.014934	2.21E-05	676				

Shape asymmetries
The results of ANOVA are shown in Table 1. Both the effect of laterality (DA) and the interaction individual*laterality (FA) appeared statistically significant, although the major contribution was those of DA (77.9% *versus* 8.9%).

PCA
PCA reflected that a 64.3% of the total observed variation was explained for the first two main Principal Components (PC) (PC1+PC2=44.42%+19.91%). According to the representation of bending energy (Figure 3), shape changes affect the lacrimal edges –*margo medialis*, with a contraction– and temporal –*margo lateralis*, with an expansion–.

Discussion

Some recent studies reveal that functional lateralization is present in many animal species. Some authors even suggest that all vertebrates they share a left hemispheric specialization for processing specific objects and sequential tasks, and a hemispheric specialization right for visual processing tasks (Llorente et al. 2008). This behavioural lateralisation could suggest advantages at the individual level how to improve neural processing for motor tasks. For example, the degree of lateralization could be positively related to the motor complexity of a task. Some evidence of this would be that strong

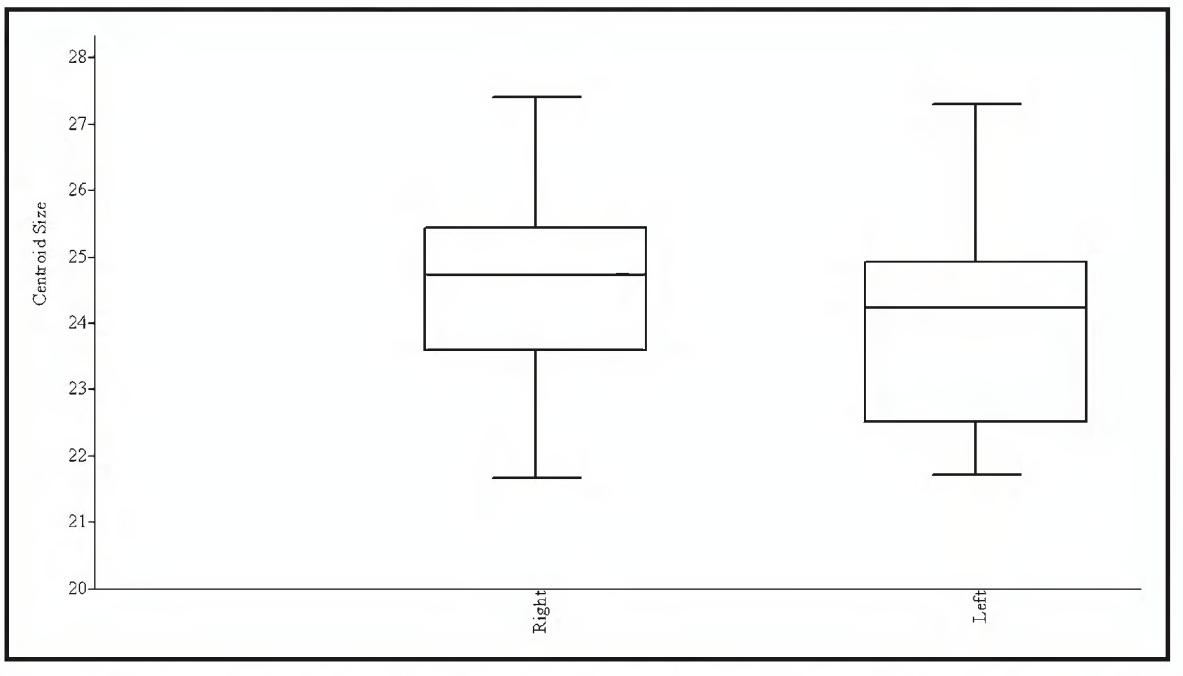

Figure 2. Box-whisker diagram for the centroid size between the right and left orbit, reflecting statistically significant differences. Each rectangle is divided by a horizontal segment indicating where the median is positioned. The whiskers have an extension limit, which in the case under study did not present any out-of-range data. Although the difference was small, there were statistically significant differences (W=287, p=0.0036), with the right size orbit being about a 1.2% larger.

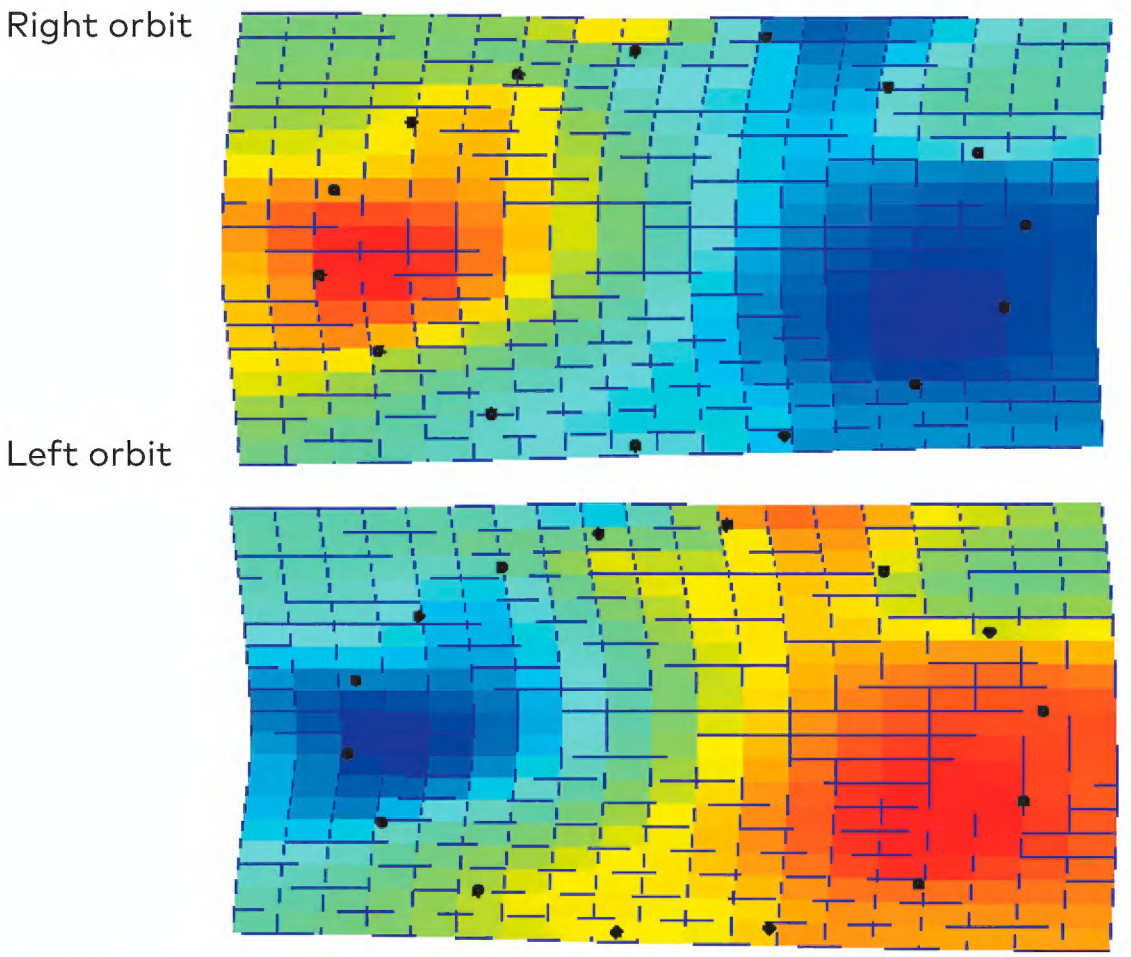

Figure 3. Representation of bending energy (thin plate spline), which allows to appreciate shape changes as forces acting on a mesh that deforms according to the direction (negative –right orbit- or positive –left orbit-). It can be said that shape changes affect the lacrimal edge –with a contraction, bluish coloration– and the temporal –with an expansion, reddish coloration– as result of local orbital deformations.

individual lateralization in primates is associated with tool use and complex food processing (Corp and Richard 2002).

Most primates depend on high-sharp vision, based mainly on frontally placed eyes, retinal specializations, and binocular vision, which ensures that the image is placed in or near the centre of the fovea (Heesy 2007; Jacobs 2008) (Braccini et al. 2012). Some few laterality studies have shown differences between the right and left eyes in non-human primates (Fagot and Vauclair 1991). In the case of this study, lateral orbital differences appear to be demonstrated for the genus *Saguinus*, which show both a size and a shape orbital asymmetry. A morphological lateralization is fixed, occurring on the same side, being right orbita larger. Conspicuous asymmetry was absent. Larger right orbits has been described in humans (Seiji et al. 2009; Lepich et al. 2017), so the detected asymmetry can be assumed as a normal anatomic adaptative pattern in other primates, as it is the case. The aetiology of this asymmetry remains unclear. In authors' opinion, it could represent a visual lateralization to direct exactly towards different targets, such as food, tree branches or other individuals to socialize, fight or defend themselves. In this work, the authors demonstrate not only that these individual lateralizations exist, but also that they are provided with a directionality at the population level. Sociability and gregarious behaviour could have facilitated

selective pressures when it came to aligning the direction of orbital asymmetries in most individuals *Saguinus* populations. Now it would be interesting to study whether animals with a dominant eye motor present laterality and/or perceptual laterality.

Acknowledgments

The authors thank Javier Quesada for allowing us access to the mastozoological collection of the *Museu de Zoologia* in Barcelona (Catalonia).

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